Functional and causal aspects of nest distribution in colonies of the sandwich tern (Sterna s. sandvicensis Lath.)

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SUMMARY

I. Introduction.

The main part of this study is an attempt to investigate whether in the sandwich tern colonial nesting enhances reproductive success, and if so how this comes about (chapter II). Besides, attention is paid to the behavioural causation of colonial nesting (chapter III). Considering the various ways in which colonial nesting might influence success, a study of function would ideally require a comprehensive study of all environmental factors. Although the relationship between nest distribution and several environmental factors will be touched upon in this study, my concern has been primarily with predation. This choice has been inspired by the work done by TINBERGEN and co-workers studying nest distribution in gulls.

According to TINBERGEN and co-workers, the spatial pattern of nest distribution in a black-headed gull colony should be regarded as a consequence of two opposing tendencies, 'clustering' and 'spacing-out', which both have an anti-predator function: Nest spacing assists concealment of the nests which in turn lowers the risk that eggs and chicks are discovered by predators, while clustering has the advantage that a predator can be simultaneously attacked by a large number of breeding birds.

Similarities in behaviour and nest distribution of Larid species suggest that the majority of tern and gull species of the northern hemisphere defend their brood against predators in a basically similar way. However, there are some exceptions among which is the sandwich tern. Sandwich terns nest at pecking distance of each other, the nesting area is rather conspicuous and the birds are not very inclined to attack predators. This aberrant behaviour cannot be explained by the absence of predators for a variety of predator species has been recorded from sandwich tern colonies.

In the case of the sandwich tern there is another point of interest which might be related to predation. Sandwich terns tend to nest in association with common terns, arctic terns and black-headed gulls. It has been suggested that the sandwich tern might gain protection against predators through the aggressiveness of these neighbours. However, it has also been noted that black-headed gulls take a heavy toll from the terns by stealing eggs, chicks and fish.

II. Functional aspects of nest distribution.

A large number of sandwich tern nests has been under continuous observation. For each of these nests reproductive success has been determined. Clutch size, group synchronization, nest position (density, inter-nest distance and central vs peripheral position), group size, colony size and island synchronization were related independently of each other to success. The influence of age differences and environmental factors correlated with the season were excluded from the analysis as much as possible. Except for group size and central vs peripheral nest position, all aspects mentioned above were correlated with hatching and/or fledging success.

The sandwich tern population at Griend consists of two groups of breeding birds, the recidivists and the recruits, which are different with respect to their date of egg-laying. The recruits are strikingly less successful than the recidivists. This can be partly explained by differences in clutch size, group synchronization, nest position and colony size. However, other factors such as environmental influences correlated with the season must play a role as well.

Data on mortality agents collected between 1966 and 1972 showed that mortality

of eggs and chicks was caused by predation (eggs 14.3%, chicks 11.7%), high tides (eggs 3.8%), hatching failure (eggs 6.9%), food shortage, diseases and physical defects (together 33.0% of chicks).

Black-headed gull, herring gull, great black-backed gull, oystercatcher, arctic skua, short-eared owl and several raptor species have been recorded in the sandwich tern colonies on Griend. Black-headed gull, herring gull and great black-backed gull were the only species preying upon the brood of the sandwich tern in any important way. Only a small proportion of the total number of gulls present on the island took part in predation on the brood of the terns. In the case of the black-headed gull the number of predators tended to increase in the course of the season. The number of herring- and great black-backed gulls preying upon the sandwich tern was limited by inter-specific aggression. Black-headed gulls have been recorded to rob eggs and chicks; herring- and great black-backed gulls mainly robbed chicks. A relatively high proportion of the eggs and chicks robbed by black-headed gulls should be regarded as potentially non-viable. Herring gulls and great black-backed gulls, however, took potentially viable chicks from the population. Considering two years of observation together, the influence of predation by black-headed gulls and herring gulls (great black-backed gulls included) on the breeding success of the sandwich tern was roughly the same.

Piracy by black-headed gulls on the food of the sandwich tern influences chick mortality when food gets short in a long lasting period of stormy weather. However, such periods are rare in the hatching season of the terns.

With respect to predation and food piracy the situation on Griend can be regarded as representative for most other colonies in the Netherlands.

To a predator which endangers the brood only, sandwich terns react with sitting down on the nest, threatening from a sitting position. To a predator which is a danger to the brood and to the adults, the terns react with flying up. In reaction to a predator which endangers only the adults, flying up from the nests, followed by escape behaviour is shown. Sometimes the predator is attacked from the air, but usually the attack frequency and intensity is low. The tendency of the terns to attack a predator strongly increases after they have left the nest shortly after hatching.

Common tern and black-headed gull tend to fly up in reaction to nearly all predator species. Predators of the brood are vigorously attacked.

The anti-predator behaviour of the sandwich tern defends the brood effectively against black-headed gulls, oystercatchers, herring gulls and great black-backed gulls. It gives little protection to the brood when avian or mammalian ground predators are involved which endanger both adults and brood.

The behaviour of predators reacting to the attacks of common tern, black-headed gull and sandwich tern mainly depends on attack frequency and intensity. Several predator species are successfully driven off from the nesting area by the combined attacks of the different breeding birds. The protective influence for the sandwich tern of common terns and black-headed gulls nesting in the neighbourhood has been substantiated in the case of predation by black-headed gulls, herring gulls and great black-backed gulls.

The discussion deals with (a) the mechanisms through which the various aspects of nest distribution might reduce predation, (b) the advantages and disadvantages of associative nesting with another species and (c) the selective advantage of the sandwich tern nest distribution pattern with respect to some environmental factors other than predation.

In the Griend situation the advantage of nesting together with black-headed gulls very likely outweighs its disadvantages. In colonies where the sandwich tern has to cope with mammalian ground predators, associative nesting has a number of advantages in addition to the ones established for the Griend situation. Therefore, it is concluded that associative nesting with common terns and black-headed gulls must be advantageous for the sandwich tern in general.

It is suggested that the nest distribution pattern of the sandwich tern and behaviour aspects related to it have evolved under the pressure of at least three different factors: food, predation and tidal movements. Exploitation of food resources may have selected for colonial nesting. Nesting aggregations will attract predators. This may have led to a selection pressure for choosing a habitat in which mammalian ground predators are scarce. However, the habitat chosen introduced the danger of high tides, which in turn may have selected for special behaviour adaptations, such as little or no attachment to the site of the previous year, selection of relatively high nesting places and the possibility for chicks to move within the area. The remarkably high nest density of the sandwich tern may have evolved as a consequence of the need for breeding synchronization. However, a shortage of nesting places safe from high tides may have selected for dense nesting as well.

III. Causal aspects of nest distribution.

This section deals with the question of how behaviour patterns leads to the spatial and temporal nest distribution pattern and to associative nesting in the sandwich tern.

Throughout the pre-laying period the terns of the Griend population go through a number of successive stages which are characterised by an increase of group density and an increase of nesting and aggressive activities. House-hunting individuals select a nesting site at very short distance of nesting conspecifics (clustering), but territorial aggression prevents them from coming too close (spacing out). There is a special relationship between incubating and non-incubating individuals; the sitting position of incubating birds seems to inhibit aggression of non-incubating individuals. Differences in minimum inter-nest distance between peak -and tail breeders of a group are explained by behaviour differences which are related with differences in phase of breeding of neighbouring pairs at the moment of nest site selection. Experiments with sandwich tern dummies have thrown some light on the influence of size and density on group attractiveness. The nature of the reactions of the terns to the dummies is investigated.

The possible ways in which synchronization of egg-laying of the island population and of separate groups may be effected are discussed.

Evidence is put forward which support the idea that associative nesting of sandwich terns with common terns and black-headed gulls is the result of interspecific attraction. An attempt to manipulate the distribution of sandwich terns on the island by placing black-headed gull dummies in the area was unsuccessful. This failure of the black-headed gull dummies, in sharp contrast to the effectiveness of the similarly made sandwich tern dummies, leads to the supposition that the terns make higher demands upon conformity with the living bird for the gull dummies than for the tern dummies. This is explained by differences in the degree to which the recognition of conspecifics and other species is based on detailed learning.